

SQ-Phenology: BioMA-SiriusQuality component of phenology

Loïc Manceau, Pierre Martre

LEPSE, Univ. Montpellier, INRA, Montpellier SupAgro, Monptellier, France (pierre.martre@inra.fr; http://www1.clermont.inra.fr/siriusquality/)

Documentation version	component version	Last modified on	Component status	Component doi
1.0	1.0	07/31/2018	Development	10.15454/1.5330248194751306E12

How to cite: Manceau L, Martre P (2018) *SQ-Phenology*: BioMA-*SiriusQuality* component of phenology. Doi: 10.15454/1.5330248194751306E12.

Summary

This document describes the procedure used in the *SQ-Phenology* crop model component to determine, the timing of the wheat developmental phases, the Phyllochron, the number of leaves on main-stem, the final leaf number and the number of tillers. Vernalization progress may be taken into account depending on the considered variety. The model is integrated in the wheat crop model *SiriusQuality2* (*Brooking et al 1995; Jamieson et al 1995b; Jamieson et al 1995a; Jamieson et al 1998b*) as an independent component. This component is developed in the public domain software framework <code>BioMA</code> (Biophysical Model Applications). BioMA is developed using Microsoft C# language in .Net framework (version 4.5). The component was coded using the development environment Microsoft Visual Studio 2013. A console application is available to enlighten the practical use of the component.



Contents

Sur	nmary	1
	Theoretical background	
2.	Overview of the calculation procedure	4
3.	Sowing date correction for phyllochron	6
4.	Vernalization progress and potential final leaf number	7
5.	Phase update and final leaf number	9
6.	Leaf number on main-stem	12
7.	Flag leaf state update	12
8.	Phyllochron	12
9.	Shoot number	15
10.	Zadok stages	15
11.	References	19
12.	Appendix	22



1. Theoretical background

Responding to environmental factors the apical meristem of the wheat shoot switches from a vegetative phase where it produces leaf primordia to a reproductive phase where it produces floral primordia. The successive appearance of leaves on the main-stem and tillers is the expression of the vegetative development, while anthesis is a particular stage in the reproductive development of wheat plants. Vegetative and reproductive development are coordinated and overlap in time (Kirby, 1990; Hay & Kirby, 1991), so that much of the reproductive development occurs early in unison with vegetative development. This means that, as far as timing of events is concerned, vegetative and reproductive processes are not independent. Within this framework, in the phenology model proposed by (Jamiesonet al., 1998), the variations associated with vernalization requirement and daylength sensitivity are described in terms of primordium initiation, leaf production, and final main-stem leaf number.

The duration of seven developmental phases are simulated (Sowing to Emergence, Emergence to Floral Initiation, Floral Initiation to Heading, Heading to Anthesis, Anthesis to End of Cell Division, End of Cell division to End of Grain Filling, End of Grain Filling to Maturity). The growth timing is parametrized as a function of the vernalization progress, the number of leaves on main-stem compared to the final leaf number, or the accumulated thermal time. Alternatively, nine Zadok or pseudo-Zadok stages are determined.

The leaf production phase is modeled based on two independently controlled processes, leaf initiation (primordia formation) and emergence (leaf tip appearance) rates and organ identity defining the fate of the apex primordia whether vegetative or floral. The interaction between these processes leads to the determination of the final number of leaves that will be produced on the main-stem.

Leaf production may follow a segmented linear model in thermal time (Boone et al., 1990; Jamieson et al., 1995; Slafer & Rawson, 1997; González et al., 2002) corrected by a surrogate for the apex-air temperature effect which depends on sowing date. Leaf production can also depend on the soluble carbohydrate economics (ref). The Photothermal Quotient (PTQ) was found to well encode the balance between photosynthetic offer (or amount of intercepted light) and growth demand (or accumulated thermal time).



At any time during vegetative development apex primordia number is calculated through a simple metric relationship with leaf number (Kirby, 1990). Concomitant processes governing apical progress towards a reproductive state and defining the final leaf number (i.e. vernalization requirements and photoperiodic responses) are modeled sequentially.

Previous work indicates that the vernalization requirement of some winter wheat genotypes can be eliminated or greatly reduced by a prolonged exposure to short photoperiods (Evans, 1987; Dubcovsky *et al.*, 2006), a process referred in the literature as short day vernalization. The photoperiodic effect on the vernalization rate is likely to involve a quantitative interaction with temperature rather than a complete replacement of the vernalization requirement (Brooking & Jamieson, 2002; Allard *et al.*, 2012).

The crop responds to daylength only once vernalization is complete (or at emergence for a spring cultivar for which the vernalization routine is skipped). It is assumed that daylength sensitivity leads to an increase in the number of leaf primordia resulting from the vernalization routine. If the daylength of the day when vernalization is completed exceeds a given value, then the final number of leaves is set to the value calculated at the end of the vernalization routine (Brooking *et al.*,1995). If not, Brooking *et al.* (1995) have shown that the final leaf number is determined by the daylength at the stage of two leaves after the flag leaf primordium has been formed.

2. Overview of the calculation procedure

Figure 1 shows the flowchart of the *SQ-Phenology* component. It is composed of nine simple strategies and a composite one. First, the sowing correction for phyllochron is calculated. Then the potential final leaf number is assessed, the vernalization may progress (CalculateVernalisationProgress), the plant developmental phase is updated and the final leaf number is calculated (UpdatePhase). If the anthesis stage is not reach yet, the leaf number is calculated and the state of the flag leaf is updated. It exists two parametrizations of the phyllochron using the Phototehermal quotient or the segmented linear model with sowing date correction. Finally, the Zadok stage is determined, the number of tillers is calculated (CalculateShootNumber) and results are exported via the composite class. This procedure is called daily. In what follows each section refers to one of the strategies described above.



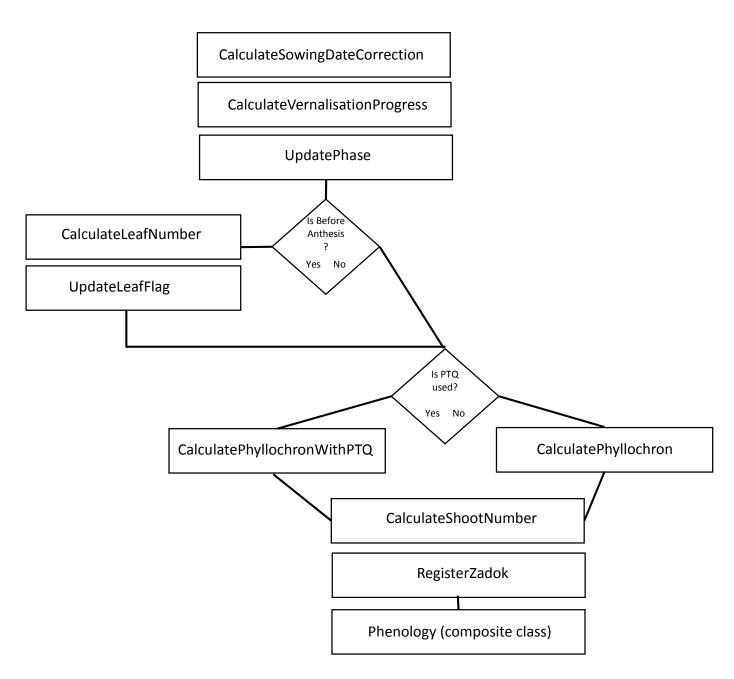


Figure 1. Shema of the BioMA-SiriusQuality SQ-Soil-Phenology component.



3. Sowing date correction for phyllochron

Many studies have shown that phyllochron depends on the sowing date, several authors have discussed putative physiological causes of theses variations (Slafer & Rawson, 1997; McMaster *et al.*, 2003); while others have shown that most of the observed variations in phyllochron are due to apex-air temperature differences (Vinocur & Ritchie, 2001; Jamieson *et al.*, 2008). In Sirius, as a surrogate for the apex-air temperature correction, for a winter sowing (day of the year 1 to 90 for the Northern hemisphere), the phyllochron decreases linearly with the sowing date and is minimum until mid-July for the Northern hemisphere (day of the year 200):

$$Phyll_{SD} = \begin{cases} Phyll_{par} \times \left(1 - R_p \times Min(SD, SD_{w/s})\right), & 1 \leq SD < SD_{S/A_nh} \\ Phyll_{par}, & SD \geq SD_{S/A_nh} \end{cases}$$
(1)



where SD is the sowing date in day of the year; $Phyll_{par}$ is a varietal parameter defining the phyllochron for autumn sowing; R_P is the rate of decrease of $Phyll_{SD}$ for winter sowing; $SD_{W/S}$ and SD_{S/A_nh} are the sowing dates for which $Phyll_{SD}$ is minimum and maximum, respectively. Similarly, in the Southern hemisphere where seasons are the opposite the correction becomes:

$$\begin{cases} Phyll_{SD} = \\ Phyll_{par} \times \left(1 - R_p \times Min(SD - SD_{S/A_Sh}, SD_{w/s})\right), & SD > SD_{S/A_Sh} \\ Phyll_{par}, & 1 \leq SD \leq SD_{S/A_Sh} \end{cases} (2)$$

 SD_{S/A_sh} has a value of 151 days and is defined as the sowing date for which $Phyll_{SD}$ is maximum in the southern hemisphere.

4. Vernalization progress and potential final leaf number

At any time during vegetative development apex primordia number (*PN*) is calculated through a simple metric relationship with leaf number (Kirby, 1990) under the assumption that the apex contains *PNini=4* primordia at emergence and that they accumulate at twice the rate of leaf emergence (Brooking *et al.*, 1995; Jamieson *et al.*, 1995):

$$PN = 2 \times LN + PNini \tag{3}$$

With LN the number of emerged leaves on main-stem.

Concomitant processes governing apical progress towards a reproductive state and defining the final leaf number (i.e. vernalization requirements and photoperiodic responses) are modeled sequentially. In the strategy described here only vernalization is considered, photoperiodic response will be presented in the next section.

Vernalization commences once the seed has imbibed water. Previous work indicates that the vernalization requirement of some winter wheat genotypes can be eliminated or greatly reduced by a prolonged exposure to short photoperiods (Evans, 1987; Dubcovsky *et al.*, 2006), a process referred in the literature as short day vernalization. The vernalizing effect of short days was introduced in *SiriusQuality*2 to improve the simulation of anthesis date in the hot-serial-cereal experiment (White *et al.*, 2011).

The daily vernalization rate ($V_{\rm rate}$) increases at a constant rate (VAI) with daily mean soil or canopy temperature ($T_{\rm shoot}$) from its value (VBEE) at the minimum vernalizing temperature ($T_{\rm min}^{\rm ver}$) to a maximum for an intermediate temperature ($T_{\rm int}^{\rm ver}$). Above this temperature $V_{\rm rate}$



reduces to zero at the maximum vernalizing temperature (T_{max}^{ver}) . The value of T_{shoot} is the soil temperature from the beginning of emergence to the time when three leaves have emerged. For further phases the canopy temperature, calculated in the $SQ_EnergyBalance$ component, is considered. TT_{shoot} is corrected by the plant response with à 0°C base temperature. The photoperiodic effect on the vernalization rate is likely to involve a quantitative interaction with temperature rather than a complete replacement of the vernalization requirement (Brooking & Jamieson, 2002; Allard $et\ al.$, 2012). It is modelled following Sirius vernalization framework, with the assumption that the effectiveness of short days decreases progressively as photoperiods increase from DL_{min}^{vern} (set at 8 h) to DL_{max}^{vern} (set at 15 h):

$$V_{rate} = \begin{cases} VAI \times TT_{shoot} + VBEE, & T_{min}^{ver} \leq TT_{shoot} \leq T_{int}^{ver} \\ 0, (VAI \times T_{int}^{ver} + VBEE) \\ \times \left(1 + \frac{T_{int}^{ver} - TT_{shoot}}{T_{max}^{ver} - T_{int}^{ver}} \times \frac{DL_{eff}^{ver} - DL_{min}^{ver}}{DL_{max}^{ver} - DL_{min}^{ver}} \right), & T_{int}^{ver} < TT_{shoot} < T_{max}^{ver} \end{cases}$$

$$(4)$$

Where the effective photoperiod is:

$$DL_{eff}^{ver} = Max(DL_{min}^{ver}, \min(DL_{max}^{ver}, DL))$$
(5)

With DL the day length and VAI and VBEE two varietal parameters. The progress toward full vernalization (V_{prog}) is simulated as a time integral:

$$V_{prog} = \sum_{day=1}^{n} V_{rate} \text{ with } V_{prog} \in [0, 1]$$
 (6)

Two varietal parameters define the minimum (L_{min}^{abs}) and maximum (L_{max}^{abs}) number of leaves that can emerge on the main-stem. The model assumes that plants start their life with a high potential leaf number (LN_{pot} set to an initial value of L_{min}^{abs}) which decreases with vernalization progress:

$$LN_{pot} = L_{max}^{abs} - (L_{max}^{abs} - L_{min}^{abs}) \times V_{prog}$$
(7)

Vernalization is completed when one of the three conditions is met. Either $V_{\rm prog}$ has reached a value of 1, LN_{pot} has reached a value that equals L_{min}^{abs} , or has reduced to PN. These primordia are all assumed to produce leaves.



5. Phase update and final leaf number

Different conditions drive the transition from one phase to another. Most of the time, changes happen when the physiological thermal time of the organs (apex or grain) exceeds a certain value fixed by a parameter. In case of the transition from emergence to floral initiation the vernalization progress, the photoperiod and the final leaf number are involved.

The pre-emergence phase (Sowing to Emergence) ends when the shoot thermal time accumulated since sowing exceeds the parameter *Dse* which may differ between cultivars (Weir *et al.*, 1984). The apex thermal time is calculated on the basis of the plant physiological response to mean shoot temperature in the *SQ-ThermalTime* component with a base temperature of 0°C. The shoot temperature is taken to the value of the soil surface until *MaxLeafSoil=4* leaves have emerged on main-stem (in fact 3 leaves are fully emerged and the tip of the forth is just visible) and subsequently to the canopy temperature, the latter being determined in the *SQ-EnergyBalance* component.

If the plant is not vernalizable (i.e spring cultivars) the floral initiation occurs just after the emergence phase. In the other case photoperiod has to be taken into account. The crop responds to day length (DL) only once vernalization is complete. It is assumed that DL sensitivity leads to an increase in the number of leaf primordia resulting from the vernalization routine. DL is calculated in the SQ-Meteorology component. If DL of the day when vernalization is completed exceeds a given value (DL_{sat}), then the final leaf number on main-stem (LN_f) is set to the value calculated at the end of the vernalization routine (Brooking $et\ al.$, 1995) and the floral initiation is reached. For DL shorter than DL_{sat} , Brooking $et\ al.$ (1995) have shown that LN_f is determined by DL at the stage of two leaves after the flag leaf primordium has been formed. This creates the need for an iterative calculation of an approximate final leaf number (LN_{app}) that stops when the required leaf stage is reached:

$$LN_{app} = Max(LN_{pot}, LN_{pot} + SLDL \times (DL_{sat} - DL))$$
(8)

where *SLDL* is a varietal parameter defining the day length response as a linear function of *DL*. The attainment of the stage "two leaves after flag leaf primordium" is reached when half of leaves have emerged (Brooking *et al.*, 1995):



$$0.5 \times LN_{app} \le LN$$
, then $LN_f = LN_{app}$ (9)

With *LN* the leaf number on main-stem of the considered day. When this condition is fulfilled, transition to floral initiation is completed.

The heading (from the time of emergence of tip of the head from the flag leaf sheath to when the head has completely emerged) and the flowering are modeled in a similar way. Estimation of the heading date is performed only if the Zadok stage 39 (Flag leaf ligule just visible) has been registered (see section 10). The thermal time duration of these two periods since the flag leaf ligule emergence ($TT_To_Heading$ and $TT_To_Anthesis$) are proportional to the phyllochron (Brooking et al., 1995) and phyllochronic durations are set as non-varietal parameters:

$$TT_To_Heading = (PFLLAnth - PHEADANTH) \times Phyll_{SD}$$
(10)

$$TT_To_Anthesis = PFLLAnth \times Phyll_{SD}$$
 (11)

Where *PFLLAnth* and *PHEADANTH* are the phyllochronic duration of the period between the flag leaf ligule appearance and anthesis and the phyllochronic duration between heading and anthesis, respectively.



After anthesis, the development continues until the endosperm cell division phase. The later lasts a grain thermal time duration of Dcd. Grain thermal time is defined as the physiological thermal time accumulated by the shoot since the beginning of the anthesis. Then, grains are filled until completion (End of Cell Division to End of Grain Filling phase). This phase lasts a duration of *Dgf* (varietal parameter) or until the green area index of the plant equals zero. The grains are finally considered mature when the thermal time accumulated since the beginning of the end of grain filling exceeds the varietal parameter *Degmf*. In *SiriusQuality2* this drying phase is optional.

In *SiriusQuality2* phases are identified by number. Table 1 summarize the different phases and the value of their corresponding code.

Sowing	0		
Emergence	1		
Floral Initiation	2		
Heading	3		
Anthesis	4		
End of Cell Division	4.5		
End of Grain Filling	5		
Maturity	6		

Table 1. *SiriusQuality2* developmental phases and their corresponding code. See section 10 for definitions.



6. Leaf number on main-stem

Between sowing and anthesis the leaf number (LN) is incremented proportionally to the leaf appearance rate under the influence of the daily apex thermal time (TT_{shoot}):

$$LN = LN + \frac{TT_{shoot}}{Phyll} \tag{12}$$

With Phyll being the Phyllochron (see section 8).

7. Flag leaf state update

For the purpose of making the leaves stop to emerge, the time when the flag leaf ligule appears has to be identify. This moment is registered when LN becomes larger or equal to LN_f (see section 5).

8. Phyllochron

7.1 Original parameterization

Originaly in *SiriusQuality2*, leaf production follows a segmented linear model in thermal time (Boone *et al.*,1990; Jamieson *et al.*, 1995; Slafer & Rawson, 1997; González *et al.*, 2002). The first two leaves appear more rapidly than the next six, and then leaf appearance slows again for the subsequent leaves independently of the total number of leaves produced. As a result, the phyllochron (or inverse of the leaf appearance rate) is expressed as follows:

$$Phyll = \begin{cases} Pdecr \times Phyll_{SD}, & LN < LN_{decr} \\ Phyll_{SD}, & LN_{decr} \leq LN < LN_{incr} \\ Pincr \times Phyll_{SD}, & LN \geq LN_{incr} \end{cases}$$
(13)

Where $Phyll_{SD}$ is the genotypic parameter defining the phyllochron corrected by sowing date effects to mimic an apex-air temperature difference correction (see section 1). Other parameters are non-varietal. If the actual number of visible leaves on main-stem (LN) is lower than $LN_{decr}=3$ the phyllochron is decreased by Pdecr. If it is larger than $LN_{incr}=8$ it is increased by Pincr. Note that LN can be seen as the Haun stage.

For test purposes it is possible to not apply the $Phyll_{SD}$ correction. The Phyllochron then writes:



$$Phyll = \begin{cases} Pdecr \times Phyll_{par}, & LN < LN_{decr} \\ Phyll_{par}, & LN_{decr} \leq LN < LN_{incr} \\ Pincr \times Phyll_{par}, & LN \geq LN_{incr} \end{cases}$$
(14)

And, for example, it is possible to work with a linear model of leaf appearance rate by setting *Pdecr* and *Pincr* value to the unity. A special BioMa strategy is dedicated to this calculation, but the strategy is not mention in this document for the sake of clarity.

7.2 Calculation from Photothermal Quotient (PTQ)

This parametrization of the phyllochron relies on four hypothesis: (1) LAR (leaf appearance rate or inverse of the phyllochron) depends on the supply-to-demand ratio for soluble carbohydrate, estimated by the ratio of intercepted light to thermal time; (2) the demand for soluble carbohydrate is proportional to plant size and this proportionality can be approximated by the green area index; (3) soluble carbohydrates in the plant provide a buffering capacity to fluctuating environments in the field; and (4) leaves are able to maintain a minimum rate of development. The model is given as:

$$\frac{1}{Phyll} = LAR = \frac{LAR_{min} + \left(\frac{LAR_{dif} \times PTQ}{PTQ_{hf} + PTQ}\right)}{\alpha \times GAI_{eff}}$$
(15)

Where $PTQ = \overline{I_{\rm int}}(d)/\overline{T_{\rm t}}(d)$ with $\overline{I_{\rm int}}(d)$ (MJ PAR m⁻² (ground)) is the cumulative PAR intercepted by the canopy during the period d, $\overline{T_{\rm t}}(d)$ (°Cd) is the thermal time accumulated during the period d, $\overline{\rm GAI}_{\rm eff}$ (m⁻² (leaf) m⁻² (ground)) is the average green area fraction over the period d, and α (-) is an empirical parameter that scales carbon demand to GAI. Parameters LAR_{min}, LAR_{dif}, and PTQ_{hf} are as in Eq. (3). In Eq. (4) LAR tends to infinite when GAI tends to 0. Therefore, a minimum value of $\overline{\rm GAI}_{\rm eff}$ was considered as the potential GAI when Haun stage = 3 and first tiller appear. $\overline{\rm GAI}_{\rm eff}$ is given as:



$$\overline{\rm GAI}_{\rm eff} = \begin{cases} {\rm LN}_{\rm eff} \times A_{\rm L_{\rm juv}}^{pot} \times {\rm PD} \times 10000, & {\rm LN} < {\rm LN}_{\rm eff} \\ \overline{\rm GAI}(d), & {\rm LN} \ge {\rm LN}_{\rm eff} \end{cases}$$
(16)

where, $A_{\rm L_{juv}}^{pot}$ (cm²) is the potential surface area of juvenile leaves, as defined in the *SiriusQuality* leaf growth model (*Martre and Dambreville*, 2018), PD (plant m⁻²) is the plant density, LN (leaf main stem⁻¹), is the number of main stem emerged leaves (leaf main stem⁻¹), and $\rm LN_{eff}$, the number of main stem leaves above which the demand for respiration increases relative to sink formation. The 10000 multiplying allows converting cm² to m².

In Eq. (5) environmental variables are averaged over several days to account for the buffering effect of stored soluble carbohydrates. The parameter d was set equal to 70°Cd (*Lattanzi et al., 2005; Rickman et al., 1985*). The fraction of light intercepted by the crop during the period d is given as (Monsi and Saeki, 2005):

$$\overline{I_{\text{int}}}(d) = \sum_{i=1}^{d} I_0(i) \left(1 - e^{-K_{\text{L}}\text{GAI}(i)}\right)$$
(17)

where, I_0 (MJ PAR m⁻² (ground) d⁻¹) is the incident daily PAR and $k_{\rm L}$ (m² (ground) m⁻² (leaf)) is the light extinction coefficient (set equal to 0.45, Thorne et al., 1988). The thermal time during the period d (MJ PAR m⁻² (ground)) is given as:

$$\overline{T_{t}}(d) = \sum_{i=1}^{d} TT_{shoot}(i)$$
(18)



9. Shoot Number

The potential number of shoots (main stem + tillers) per plant (NT) is first calculated as a function of the number of leaves emerged on main-stem (LN). After (Kirby, 1985) it follows a Fibonacci sequence:

$$NT_{LN+2} = NT_{LN+1} + NT_{LN} (15)$$

 NT_{LN+2} corresponds to the stage where two extra leaves have appeared and equals the number of tillers during the previous stage (when LN+1 leaves were on the main-stem) summed with the original number of tillers (when the number of leaves was LN). The evaluation of NT is recursive and the number of tillers corresponding to LN=1 and LN=2 are $NT_1=1$ and $NT_2=1$, repectively.

The shoot number is then multiplied by the sowing density to obtain a mean shoot number per square meter (NT_{pot}). As it is unusual to observed more than three fertile tillers in field conditions due to competition for light interception, the maximum shoot density is limited by a user parameter (TargetFertileShoot) and the actual shoot density (NT_{act}) is:

$$NT_{act} = Min(NT_{not}, TargetFertileShoot)$$
 (16)

10. Zadok stages

In addition to the developmental phases presented in section 5, Zadok stages (or equivalent) are registered along with the cumulated shoot physiological thermal time from sowing to the beginning of the stage as well as the date the stage has been reached. Table 2 enumerates the considered developmental stages and their definition.

ZC_00_Sowing	Germination (Zadok 00 to 09): From Dry seed to Leaf just at coleoptile tip
ZC_10_Emergence	Seeding development (Zadok 10 to 19): For Zadok stage 10 the tip of the first leaf is visible on main stem
EndVernalisation	Tillering (Zadok 20 to 29): End of the vernalization period and Main shoot only
ZC_21_MainShootPlus1Tiller	Tillering: First tiller has appeared



FloralInitiation	Apex differentiates and can become future leaves or future flowers		
ZC_22_MainShootPlus2Tiller	Tillering: Second tiller has appeared		
TerminalSpikelet	The full complement of spikelets has been initiated at the shoot apex		
ZC_30_PseudoStemErection	Stem elongation or jointing (Zadok 30 to 39): The nodes and the growing point move upward from the crown to produce long stiff stem that will carry the head. This is the first phase of that process.		
ZC_23_MainShootPlus3Tiller	Tillering: third tiller has appeared		
BeginningStemExtension	Stem elongation or jointing: The nodes from which leaves develop are telescoped at the crown during the tillering stage. Once jointing starts, the internode region elongates		
ZC_31_1stNodeDetectable	Stem elongation or jointing: The first node can be detected without dissecting the plant		
ZC_32_2ndNodeDetectable	Stem elongation or jointing: Second node can be detected		
ZC_37_FlagLeafJustVisible	Stem elongation or jointing: the tip of the last leaf just before the ear (flag leaf) is visible		
ZC_39_FlagLeafLiguleJustVisible	Stem elongation or jointing: Flag leaf ligule/collar has just appeared		
Heading	Zadok stages from 50 to 59: The heading stage extends from the time of emergence of the tip of the head from the flag leaf sheath to when the head has completely emerged but has not yet started to flower		
ZC_65_Anthesis	Flowering or anthesis (Zadok 60 to 69): Pollination and fertilization occur during this period. All heads of a properly synchronized wheat plant flower within a few days and the embryo and endosperm begin to form immediately		



	after fertilization. Flowering is half completed at Zadok stage 65
ZC_75_EndCellDivision	Milk stages (Zadok 71 to 77): Early kernel formation occurs during the milk stage. The developing endosperm starts as a milky fluid that increases in solids as the milk stage progresses. Kernel size increases rapidly during this stage. Stage Zadok 75 corresponds to the end of endosperm cell division
ZC_85_MidGrainFilling	Dough Stages (Zadok 83 to 87): Kernel formation is completed during the dough development stage. The kernel accumulates most of its dry weight during dough development. Zadok stage 85 corresponds to the soft dough, before the transport of nutriments from the leaves, stems and spike to the developing grain is completed (hard dough). During this stage the endosperm endoreduplication ends
ZC_91_EndGrainFilling	Ripening stages (Zadok 91 to 99). Zadok 91 corresponds to a hard kernel when it is difficult to separate grains by fingernail
ZC_92_Maturity	Ripening stages: Grains are dry

Table 2. SiriusQuality2 growth stages and their definition.

When no phase (see section 5) has been defined for a Zadok stage, the latter is determined from the plant Haun stage (equivalent to the number of leaf visible on main-stem) or special conditions related to the nature of the stage. Table 3 summarize the conditions to reach the different growth stages.

ZC_00_Sowing	Initial stage at the beginning of the simulation and phase =0
ZC_10_Emergence	Phase value = 1



EndVernalisation	The variety is vernalizable and $V_{prog} \ge 1$		
	or $PN \ge L_{max}^{abs}$ or $PN \ge LN_{pot}$ (see		
	equations 6 and 7)		
ZC_21_MainShootPlus1Tiller	Leaf number = 4		
FloralInitiation	Phase value = 2		
ZC_22_MainShootPlus2Tiller	Leaf number = 5		
BeginningStemExtension	The last internode created has a length larger than zero		
TerminalSpikelet	$LN = slopeTSFLN \times LN_f - intTSFLN$ (17)		
	With LN the leaf number, LN _f the final leaf number and slopeTSFLN and intTSFLN two non-varietal parameters corresponding to the slope and the intercept of the linear relationship between Haun stage at terminal spikelet and final leaf number, respectively		
ZC_30_PseudoStemErection	Four leaves before their final number have grown		
ZC_23_MainShootPlus3Tiller	Leaf number = 6		
ZC_31_1stNodeDetectable	Three leaves before their final number have grown		
ZC_32_2ndNodeDetectable	Two leaves before their final number have grown		
ZC_37_FlagLeafJustVisible	One leaf before the final number has grown		
ZC_39_FlagLeafLiguleJustVisible	Leaf number equals final leaf number		
Heading	Phase value = 3		
ZC_65_Anthesis	Phase value = 4		
ZC_75_EndCellDivision	Phase value = 4.5		
ZC_85_MidGrainFilling	Phase value = 4.5 and the accumulated shoot thermal time since anthesis is larger than the parameter <i>Der</i>		



	(Duration of the endosperm endoreduplication)		
ZC_91_EndGrainFilling	Phase value = 5		
ZC_92_Maturity	Phase value = 6		

Table 3. SiriusQuality2 developmental stages and conditions to attain them.

While phases defined in section 5 are actual benchmarks for the *SiriusQuality2* simulation, Zadok stages without phase correspondence are only used as time marker in the output files for comparison with observations.

11. References

Jamieson PD, Brooking IR, Porter JR, Wilson DR (1995a). Prediction of leaf appearance in wheat: a question of temperature. F Crop Res 41:35–44. doi: 10.1016/0378-4290(94)00102-I.

Jamieson PD, Francis GS, Wilson DR, Martin RJ (1995b). Effects of water deficits on evapotranspiration from barley. Agric For Meteorol 76:41–58. doi: 10.1016/0168-1923(94)02214-5.

Jamieson PD, Porter JR, Goudriaan J, et al (1998a). A comparison of the models AFRCWHEAT2, CERES-Wheat, Sirius, SUCROS2 and SWHEAT with measurements from wheat grown under drought. F Crop Res 55:23–44. doi: 10.1016/S0378-4290(97)00060-9.

Jamieson PD, Semenov M a., Brooking IR, Francis GS (1998b). Sirius: a mechanistic model of wheat response to environmental variation. Eur J Agron 8:161–179. doi: 10.1016/S1161-0301(98)00020-3.

Martre P, Jamieson P, Semenov MA, et al (2006). Modelling protein content and composition in relation to crop nitrogen dynamics for wheat. Eur J Agron 25:138–154. doi: http://dx.doi.org/10.1016/j.eja.2006.04.007.

Kirby EJM. 1990. Co-ordination of leaf emergence and leaf and spikelet primordium initiation in wheat. *Field Crops Research* **25**: 253-264.

Hay RKM, Kirby EJM. 1991. Convergence and synchrony-a review of the coordination of development in wheat. *Australian Journal of Agricultural Research* **42**: 661-700.

Boone MYL, Rickman RW, Whisler FD. 1990. Leaf appearance rates of



two winter wheat cultivars under high carbon dioxide conditions. *Agronomy Journal* **82**: 718-724.

Slafer GA, Rawson HM. 1997. Phyllochron in wheat as affected by photoperiod under two temperature regimes. *Australian Journal of Plant Physiology* **24**: 151-158.

González FG, Slafer GA, Miralles DJ. 2002. Vernalization and photoperiod responses in wheat pre-flowering reproductive phases. *Field Crops Research* **74**: 183-195.

Evans L. 1987. Short day induction of inflorescence initiation in some winter wheat varieties. *Australian Journal of Plant Physiology* **14**: 277-286.

Dubcovsky J, Loukoianov A, Fu D, Valarik M, Sanchez A, Yan L. 2006. Effect of photoperiod on the regulation of wheat vernalization genes VRN1 and VRN2. *Plant Molecular Biology* **60**: 469-480.

Brooking IR, Jamieson PD. 2002. Temperature and photoperiode response of vernalization in near-isogenic lines of wheat. *Field Crops Research* **79**: 21-38.

Allard V, Veisz O, Kõszegi B, Rousset M, Le Gouis J, Martre P. 2012. The quantitative response of wheat vernalization to environmental variables indicates that vernalization is not a response to cold temperature. *Journal of Experimental Botany* **63**: 847-857.

Brooking IR, Jamieson PD, Porter JR. 1995. The influence of daylength on final leaf number in spring wheat. *Field Crops Research* **41**: 155-165.

White JW, Kimball BA, Wall GW, Ottman MJ, Hunt LA. 2011. Responses of time of anthesis and maturity to sowing dates and infrared warming in spring wheat. *Field Crops Research* 124: 213-222.

Weir AH, Bragg PL, Porter JR, Rayner JH. 1984. A winter wheat crop simulation model without water or nutrient limitations. *Journal of Agricultural Science* **102**: 371-382.

Martre, P., and Dambreville A. 2017. A model of leaf coordination to scale-up leaf expansion from the organ to the canopy. Plant Physiol. pp.00986.2017.

Lattanzi FA, Shnyde H., Thornton B. (2005), The sources carbon and nitrogen supplying leaf growth: assessment of the role of store with compartmental models. Plant Physiol. 137:383-395.

Rickman, R.W., Klepper, B., and Peterson, C.M. (1985). Wheat Seedling Growth and Developmental Response to Incident Photosynthetically Active Radiation 1. Agron. J. *77*, 283–287.



Monsi and Saeki (2005), *Annals of Botany*, Volume 95, Issue 3, 1 February 2005, Pages 483–494, https://doi.org/10.1093/aob/mci047.

Kirby EJM, APPLEYARD M, FELLOWES G. 1985. Leaf emergence and tillering in barley and wheat. Agronomie, 1985, 5 (3), 193-200.



12. Appendix

Table A1. List of variables used in *SQ-Phenology* component.

Symbol	Name in the code	Unit	Description	Equa	tion Strategy
$Phyll_{SD}$	Fixphyll	°Cd/leaf	Surrogate for the apex-air temperature correction of the phyllochron parameter $(Phyll_{par})$	(1)(2)(13)(10)(11)	CalculatePhylSowingDateC orrection CalculatePhyllochron
PN	primordno	-	Apex primordia number	(3)	CalculateVernalizationProg ress
LN	LeafNumber	leaf	Number of emerged leaf on main-stem	(9)(12)(13)(14) (16) (19)	CalculateLeafNumber CalculatePhyllochron CalculateShootNumber CalculateVernalizationProg ress RegisterZadok UpdateLeafFlag CalculateLeafNumber CalculatePhyllochron



TT_{shoot}	DeltaTT	°Cd	Shoot physiological thermal time of the day	(4)(12)(18)	CalculateLeafNumber CalculateVernalizationProg ress
V_{rate}	-	1/d	Vernalization rate	(4)(6)	-
DL	DayLength	hour	Photoperiod	(5)(8)	CalculateVernalizationProg ress UpdatePhase
DL_{eff}^{ver}	DLverna	hour	Effective photoperiod	(4)(5)	CalculateVernalizationProg ress
V_{prog}	Vernaprog	-	Vernalisation Progress	(6)(7)	CalculateVernalizationProg ress UpdatePhase
LN_{pot}	potlfno	Leaf	Potential final leaf number	(7)(8)	CalculateVernalizationProg ress UpdatePhase
LN_{app}	appFLN	leaf	Approximated final leaf number	(8)(9)	UpdatePhase
LN_f	FinalLeafNumber	leaf	Final leaf number	(9)(21)	UpdatePhase UpdateLeafFlag Register Zadok



TT_To_Heading	ttFromLastLeafToHeading	°Cd	Thermal time accumulated from the emergence of flag leaf to heading	(11)	UpdatePhase
TT_To_Anthesis	ttFromLastLeafToAnthesis	°Cd	Thermal time accumulated from the emergence of flag leaf to anthesis	(10)	UpdatePhase
Phyll	Phyllochron	°Cd/leaf	Phyllochron from segmented linear model	(12)(13)(14)(15)	CalculatePhyllochron CalculateLeafNumber
LAR	LAR	leaf/°Cd	Leaf appearance rate	(15)	CalculatePhyllochronWithP TQ
PTQ	PTQ	MJ(PAR)/m²/° Cd	PhotoThrermal Quotient	(15)	CalculatePhyllochronWithP TQ CalculatePTQ
$GAI_{\it eff}$	GAILim	m²(lea f)/m²(soil)	Potential GAI when <i>LN=LNeff</i>	(15)(16)	CalculatePhyllochronWithP TQ
$\overline{\mathrm{GAI}}(d)$	GAImean	m²(lea f)/m²(soil)	Canopy Green Area Index averaged on the TTWindowForPTQ thermal time interval	(16)	CalculatePhyllochronWithP TQ CalculateGAImean
GAI	GAI	m²(lea f)/m²(soil)	Canopy Green Area Index of the day	(17)	CalculateGAImean CalculatePTQ

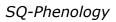


I ₀	PAR	MJ(PAR)/m²/d	Incident Photosynthetically Active Radiation of the day	(17)	CalculatePTQ
$\overline{I_{ m int}}(d)$	parInt	MJ(PAR)/m²	Intercepted Photosynthetically Active Radiation summed on the TTWindowForPTQ thermal time interval	(17)	CalculatePTQ
$\overline{T_{t}}(d)$	TTShoot	°Cd	Phsiological thermal time summed on the TTWindowForPTQ thermal time interval	(18)	CalculateGAImean CalculatePTQ
NT	Shoots	-	Shoot number (main-stem + tillers) per plant	(19)	CalculateShootNumber
NT_{pot}	-	m ⁻²	Potential shoot (main-stem +tiller) density	(20)	CalculateShootNumber
NT_{act}	CanopyShootNumber	m ⁻²	Actual shoot (main-stem +tiller) density	(20)	CalculateShootNumber



Table A2: List of parameters and constants used in the *SQ-Phenology* component. Parameter values are given for spring wheat and Yecora Rojo variety. When nothing is indicated, a Non-varietal parameter is considered.

Symbol	Name in the code	Nominal value	Unit	Description	Equation	Reference
$Phyll_{par}$	Р	120	°Cd/leaf	Phyllochron of the variety (varietal)	(1)(2)(14)	Qualset, C.O., Vogt, H.E., Borlaug, N.E., 1985. Registration of 'Yecora Rojo' wheat. Crop Sci. 25, 1130.
SD	SowingDay	80	Day of the year	Sowing date	(1)(2)	-
R_p	Rp	0.003	1/day of year	Rate of change of phyllochron with sowing date	(1)(2)	Boone <i>et al.</i> ,1990; Jamieson <i>et al.</i> , 1995; Slafer & Rawson, 1997; González <i>et al.</i> , 2002
$SD_{W/S}$	SDws	90	day of year	Sowing date at which Phyllochron is minimum	(1)(2)	Boone <i>et al.</i> ,1990; Jamieson <i>et al.</i> , 1995; Slafer & Rawson, 1997; González <i>et al.</i> , 2002
SD_{S/A_nh}	SDsa_nh	200	day of year	Sowing date at which Phyllochron is maximum in Northern hemisphere	(1)	Boone <i>et al.</i> ,1990; Jamieson <i>et al.</i> , 1995; Slafer & Rawson, 1997; González <i>et al.</i> , 2002
SD_{S/A_Sh}	SDsa_sh	151	day of year	Sowing date at which Phyllochron is maximum in Sourthern hemisphere	(2)	Boone <i>et al.</i> ,1990; Jamieson <i>et al.</i> , 1995; Slafer & Rawson, 1997; González <i>et al.</i> , 2002





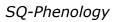
PNini	PNini	4	primordium	Number of primordia in the apex at emergence	(3)	Brooking <i>et al.</i> , 1995; Jamieson <i>et al.</i> , 1995
VAI	VAI	0.015	1/°Cd	Response of vernalization rate to temperature (Varietal)	(4)	Qualset, C.O., Vogt, H.E., Borlaug, N.E., 1985. Registration of 'Yecora Rojo' wheat. Crop Sci. 25, 1130.
VBEE	VBEE	0.01	1/d	Vernalization rate at 0°C (Varietal)	(4)	White <i>et al.</i> , 2011
T_{min}^{ver}	MinTvern	0	°C	Minimum temperature for vernalization to occur	(4)	White <i>et al.</i> , 2011
T_{max}^{ver}	MaxTvern	23	°C	Maximupm temperature for vernalization to occur	(4)	White <i>et al.</i> , 2011
T_{int}^{ver}	IntTvern	11	°C	Intermediate temperature for vernalization to occur	(4)	White <i>et al.</i> , 2011
DL_{min}^{ver}	MinDL	8	hour	Threshold day length below below which it does not influence vernalization rate	(4)(5)	White <i>et al.</i> , 2011
DL_{max}^{ver}	MaxDL	15	hour	Saturating photoperiod above which final leaf number is not influenced by day length	(4)(5)	White <i>et al.</i> , 2011
L_{max}^{abs}	AMXLFNO	24	leaf	Absolute maximum leaf number	(7)	Brooking <i>et al.</i> , 1995; Jamieson <i>et al.</i> , 1995
L_{min}^{abs}	AMNFLNO	5.5	leaf	Absolute minimum leaf number	(7)	Brooking et al., 1995; Jamieson et al., 1995



SLDL	SLDL	0.85	Leaf/h (day length)	Day length response of leaf production (Varietal)	(8)	Qualset, C.O., Vogt, H.E., Borlaug, N.E., 1985. Registration of 'Yecora Rojo' wheat. Crop Sci. 25, 1130.
DL_{sat}	MaxDL	15	hour	Saturating photoperiod above which final leaf number is not influenced by daylength	(8)	Brooking et al., 1995
PHEADANTH	PFLLAnth	2.22	Phyllochron	Phyllochronic duration of the period between flag leaf ligule appearance and anthesis	(10)	Boone <i>et al.</i> ,1990; Jamieson <i>et al.</i> , 1995; Slafer & Rawson, 1997; González <i>et al.</i> , 2002
PHEADANTH	PHEADANTH	1	Phyllochron	Phyllochronic duration between heading and anthesis	(11)	Boone <i>et al.</i> ,1990; Jamieson <i>et al.</i> , 1995; Slafer & Rawson, 1997; González <i>et al.</i> , 2002
Dse	Dse	105	°Cd	Thermal time from sowing to emergence (Varietal)	-	Qualset, C.O., Vogt, H.E., Borlaug, N.E., 1985. Registration of 'Yecora Rojo' wheat. Crop Sci. 25, 1130.
Dcd	Dcd	100	°Cd	Duration of the endosperm cell division phase	-	Boone <i>et al.</i> ,1990; Jamieson <i>et al.</i> , 1995; Slafer & Rawson, 1997; González <i>et al.</i> , 2002
Dgf	Dgf	450	°Cd	Grain filling duration from anthesis to physiological maturity (Varietal)	-	Qualset, C.O., Vogt, H.E., Borlaug, N.E., 1985. Registration of 'Yecora Rojo' wheat. Crop Sci. 25, 1130.
Der	Der	300	°Cd	Duration of the endosperm endoreduplication phase	-	Boone <i>et al.</i> ,1990; Jamieson <i>et al.</i> , 1995; Slafer &



						Rawson, 1997; González <i>et al.</i> , 2002
Degfm	Degfm	0	°Cd	Grain maturation duration from physiological maturity to harvest ripeness (Varietal)	-	Qualset, C.O., Vogt, H.E., Borlaug, N.E., 1985. Registration of 'Yecora Rojo' wheat. Crop Sci. 25, 1130.
MaxLeafSoil	MaxLeafSoil	4	leaf	Leaf number up to which the canopy temperature is equal to the soil temperature	-	Boone <i>et al.</i> ,1990; Jamieson <i>et al.</i> , 1995; Slafer & Rawson, 1997; González <i>et al.</i> , 2002
Pdecr	Pdecr	0.4	-	Factor decreasing the phyllochron for leaf number less than LN_{decr}	(13)(14)	Boone <i>et al.</i> ,1990; Jamieson <i>et al.</i> , 1995; Slafer & Rawson, 1997; González <i>et al.</i> , 2002
Pincr	Pincr	1.25	-	Factor decreasing the phyllochron fro leaf number larger than LN_{incr}	(13)(14)	Boone <i>et al.</i> ,1990; Jamieson <i>et al.</i> , 1995; Slafer & Rawson, 1997; González <i>et al.</i> , 2002
LN_{decr}	Ldecr	3	leaf	Leaf number up to which the phyllochron is decreased by Pdecr	(13)(14)	Boone <i>et al.</i> ,1990; Jamieson <i>et al.</i> , 1995; Slafer & Rawson, 1997; González <i>et al.</i> , 2002
LN_{incr}	Lincr	8	leaf	Leaf number above which the phyllochron is increased by Pincr	(13)(14)	Boone <i>et al.</i> ,1990; Jamieson <i>et al.</i> , 1995; Slafer & Rawson, 1997; González <i>et al.</i> , 2002
LN_{ieff}	LNeff	3	leaf	Number of main-stem leaves above which the demand for respiration increases relative to sink formation	(16)	ref





LAR _{min}	LARmin		Leaf/°Cd	Minimum leaf appearance rate when photothermal quotient equals zero (varietal)	(15)	ref
LAR _{dif}	LARdif		Leaf/°Cd	Value to add to ${\rm LAR_{\rm min}}$ to reach maximum leaf appearance rate when photothermal quotient tends to infinite	(15)	ref
PTQ _{hf}	PTQhf		MJ(PAR)/m²°Cd	Photothermal quotient when leaf appearance rate is half ${\rm LAR}_{\rm dif} + {\rm LAR}_{\rm min}$	(15)	ref
$A_{ m L_{ m juv}}^{pot}$	AreaSL + AreaSS		Cm ²	Potential area of small leaves (exposed sheath+laminae)(Varietal)	(16)	Qualset, C.O., Vogt, H.E., Borlaug, N.E., 1985. Registration of 'Yecora Rojo' wheat. Crop Sci. 25, 1130.
d	TTWindowForPTQ	70	°Cd	Thermal Time window for the sliding average of the PTQ calculations	(17)(18)	Lattanzi et al., 2005; Rickman et al., 1985
KL	K1	0.45	M²(soil)/m²(lea f)	Light extinction coefficient (vatietal)	(17)	Qualset, C.O., Vogt, H.E., Borlaug, N.E., 1985. Registration of 'Yecora Rojo' wheat. Crop Sci. 25, 1130.
TargetFertileShoot	TargetFertileShoot	600	Shoot/m ²	Target fertile shoot number	(20)	-
slopeTSFLN	slopeTSFLN	0.9	-	Slope of the relationship between Haun stage at terminal spikelet and final leaf number		Boone <i>et al.</i> ,1990; Jamieson <i>et al.</i> , 1995; Slafer & Rawson, 1997; González <i>et al.</i> , 2002



intTSFLN	intTSFLN	2.6	leaf	Intercept of the relationship between Haun stage at terminal spikelet and final leaf number	(21)		Boone <i>et al.</i> ,1990; Jamieson <i>et al.</i> , 1995; Slafer & Rawson, 1997; González <i>et al.</i> , 2002
-	IsVernalizable	1		Integer: 1 the plant is vernalizable, 0 it is not (Varietal)		-	Qualset, C.O., Vogt, H.E., Borlaug, N.E., 1985. Registration of 'Yecora Rojo' wheat. Crop Sci. 25, 1130.
-	Latitude	33.069	degree	Latitude of the field		-	-
PD	SowingDensity	288.0	1/m²	Density of Sowing		(16)	-